

*MEAL PATTERNS OF CATS ENCOUNTERING
VARIABLE FOOD PROCUREMENT COST*

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The meal patterns of 2 cats in a laboratory habitat with variable foraging costs were examined in a foraging paradigm in which subjects could initiate meals at any time by completing a predetermined number of bar presses (the procurement price) and then could eat any amount. From meal to meal, the procurement price either was fixed or varied among a geometric series of five prices. As the fixed price or the mean of the variable prices increased, meal frequency decreased and meal size increased; daily intake was unaffected. Within variable-price schedules, meal size was not related to the just-paid procurement price. These results suggest that cats respond to the global rather than to the local cost structure of their habitat. They appear to respond to an average of the prices encountered, initiating meals of a frequency and size appropriate to that average. This was true even when the average price was high, meals were infrequent, and thus price encounters were widely separated in time. Therefore, the time window over which the consequences of behavior can affect behavior is longer than often conceived, at least in economies in which the animal controls its intake and the frequency, size, and distribution of its meals.

Key words: food intake, meal frequency, meal size, foraging, procurement cost, cat

An efficient forager integrates information about its habitat from encounters with the available resources over time and space. Resources vary in the quantity, quality, cost of procuring access, cost of consumption, and also in their location and distribution, which influence the frequency with which each is encountered and the time and effort required to locate and travel among patches. These attributes can be simulated in the laboratory using instrumental responses (Collier & Johnson, in press). Our laboratory foraging simulation differs from the conventional operant paradigm in that the animal lives in the experimental apparatus, and the animal, rather than the experimenter, determines both the initiation and size of all meals. These parameters prove to be major variables in an animal's accommodation to the habitat. For example, when animals perform an instrumental behavior to procure access to the available food and then may eat an unlimited amount in the ensuing meal, they adjust the pattern of food intake (i.e., meal frequency and size) in such a fashion as to limit the

overall foraging cost: As the procurement price increases, meals are initiated less often and more is consumed each time. Thus, intake is conserved at a lower total cost than if meal frequency and size were unchanged as procurement price increased (Collier & Johnson, in press; Collier, Johnson, Hill, & Kaufman, 1986).

In many habitats the procurement price differs among the various kinds of food, or various patches of the same food, that are available. How are meal patterns related to procurement price in this case? Do animals respond to the immediate contingency and eat a larger meal after paying a higher price? When rats search for, and may accept or reject, sequential opportunities to eat in one of two food patches in their habitat, one of which has a higher procurement price, they eat more meals where the price is lower, but they eat the same amount per meal in both patches. Meal size in both patches increases (and total meal frequency decreases) as the *average* procurement price increases (Collier, 1982). More recently, we randomly varied the procurement price from meal to meal of the same food among five prices (Johnson & Collier, 1994). In some five-price blocks, the prices were relatively low, and in others they were relatively high. When we compared between blocks, we found the typical pattern: Rats initiated meals less frequently and ate more per meal during high-cost blocks. However, with-

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in each schedule, the size of each meal was unrelated to the procurement price for that meal. The frequency and size of meals during a variable-price schedule were not different than they were during schedules when the price was constant from meal to meal and equal to the average of the variable prices. The results of these studies suggest that one part of the information a rat has about its habitat is an average price of procuring access to food, and that this average contributes to the determination of meal size and frequency. An interesting feature of our results was that during high-cost variable-price schedules, the prices were encountered infrequently (once or twice per day); this indicates that the rat is affected by foraging prices encountered over a substantial time window, much longer than the 16- to 40-min time horizon that has been suggested in previous operant studies using deprived animals (Timberlake, Gawley, & Lucas, 1987, 1988). It should be noted, however, that in those studies, the question was how future costs, rather than past cost encounters, would affect current behavior.

Rats (*Rattus norvegicus*) and cats (*Felis domesticus*) occupy different niches, the rat being an opportunistic omnivore and the cat being a predatory carnivore (Schoener, 1971). One might conjecture that the predator would be more sensitive to the immediate cost of each prey item. In the present experiment, we ask whether cats employ the same strategy as rats when sequentially encountering food patches that vary in procurement price.

METHOD

Subjects and apparatus. Two 5-year-old, uncaged, domestic cats, 1 male (Bill) and 1 female (Presto), were used in separate experiments. Each cat was free living and had continuous access to a small room that contained its feeding apparatus and a large running wheel. During the work day (approximately 8:30 a.m. to 6:00 p.m.), each cat also had access to an adjoining large laboratory and interacted with its human occupants. The cats could not interact with each other. In a daily maintenance period of about 20 min at approximately the same time each day and when the cat was not eating, each cat was

weighed, its data were recorded, its food and water were replenished, and its equipment was cleaned and tested. Any changes in the instrumental contingencies were made at this time. If procurement was in progress at the time of maintenance, at the end of maintenance the cat was credited with the responses already made.

Bill's apparatus consisted of a Plexiglas platform (90 cm by 41 cm by 16 cm) equipped with a large bowl filled with approximately 300 g of moist cat food (Hill's CD feline canned formula). The top of the dish was level with the bottom of the platform and could be occluded by a cam-operated cover. A photocell mounted 2.5 cm above the cover monitored the presence of the cat. A T-shaped response bar (BCS Inc.) that required 0.35 N to depress was located 5 cm above and 20 cm to the left of the cover. A 2-cm cuelight was located above the response bar. During intermeal intervals, the feeder cover was closed and the cuelight was illuminated. The cat could initiate a meal by completing a number of bar presses (the procurement price), at which time the cuelight was extinguished and the cover was opened. The cat could eat any amount; the cover closed only after 10 consecutive minutes elapsed without an interruption of the photobeam, defining the end of the meal. The cuelight was reilluminated at this time, and a new meal could be initiated at any time. A microcomputer (Commodore Pet, Model 4032) recorded bar presses and photobeam interruptions and controlled the operation of the apparatus.

Presto's apparatus consisted of a Plexiglas platform (106 cm by 40 cm by 8 cm) fitted at one end with a pellet dispenser (BCS Inc.) that delivered 190-mg pellets of a nutritionally complete cat food (BioServ, Inc.) into a Plexiglas catch tray. A T-shaped response bar (BCS Inc.) that required 0.35 N to activate was centered 5 cm above the pellet tray. A 1.5-cm cuelight (the procurement light) was mounted 5 cm above the bar. A 2-cm cuelight (the consumption light) was located 9 cm above and 12.5 cm to the right of the bar. The cat could initiate a meal by responding on the bar. The first bar press caused the procurement light to be illuminated. Upon completion of the procurement price, the procurement light was extinguished and the

consumption light was illuminated, indicating that pellets could be earned; each pellet cost five bar presses. The feeder remained active until 10 consecutive minutes elapsed with no pellets earned, at which time the consumption light was extinguished. The cat could initiate a new meal at any time. An microcomputer (MIT) recorded bar presses and controlled the operation of the lights and pellet dispenser.

Procedure. Both cats had been in previous experiments and required no additional training. In this experiment they were tested with procurement prices that were fixed or that varied from meal to meal. During fixed-price schedules, the procurement price was constant for all meals. The prices were 40, 80, 160, 320, 640, 1,280, and 2,560 responses for Bill and 8, 16, 32, 64, 128, 256, and 512 responses for Presto. Each variable-price schedule consisted of a geometric series of five prices whose middle price (geometric average) was equal to one of the fixed prices; they are labeled according to the middle price. For example, the most costly variable-price schedule for Bill, VR 2,560, had prices of 640, 1,280, 2,560, 5,120, and 10,240 responses, and the least costly variable-price schedule for Presto, VR 8, had prices of 2, 4, 8, 16, and 32 responses. In each five-meal frame, the price of each meal was selected randomly without replacement from the five possible prices; thus each price appeared once over each five-meal frame, in a different random order each time.

Each cat was exposed first to the variable-price schedules, presented initially in ascending order and then once each in a random order. Then the fixed-price schedules were presented in a random order. Each schedule was in effect for at least 10 days, but sometimes a variable-price schedule lasted as long as 60 days in order to collect data on at least eight meals of each price.

Data analysis. Data from the initial, ascending-order presentations of the variable-price schedules and the 1st day each schedule was in effect are not included in the analyses presented here. We recorded daily meal frequency and food intake and the time of each procurement response for both cats. For Bill, we recorded the eating time (time the photobeam was interrupted) and the length (time from the first to last photobeam interrup-

tion) of each meal; and we calculated mean meal size (total intake divided by total meals) and eating rate (total intake divided by total eating time). The number of grams of food consumed in individual meals were estimated by multiplying the eating time for that meal by the mean eating rate. For Presto, we recorded the number of pellets earned, the bar-pressing time (excluding pauses between responses longer than 15 s), and the length (time from the first to last bar press in the presence of the consumption light) of each meal; we also calculated eating rate (pellets divided by meal length).

RESULTS

Figure 1 presents the average meal frequencies, meal sizes, and daily intakes for both cats during the fixed- and variable-price schedules. The frequency of initiating meals was a declining function, and intermeal interval length was an increasing function, of increasing cost. Meal size increased compensatorily as meal frequency declined, and total daily intake was relatively constant. The values of these variables differed between fixed- and variable-price schedules of the same average price, but the form of the functions did not. Intake in grams was different between the 2 cats, in part because Bill's food was moist and Presto's food was dry. Also, Bill was larger (approximately 4.7 kg compared to Presto's 3.6 kg), and although both cats had access to a running wheel, Presto did not use the wheel and Bill did, sometimes traveling more than a mile per day.

As price increased, the latency to initiate procurement and the time to complete the procurement requirement both increased (Figure 2). The pattern of responding during procurement was characterized by occasional long interruptions when the cat left the apparatus and wandered about the laboratory engaging in other activities. However, the median interresponse times (IRTs, Figure 2) were quite constant across schedules, indicating that, when actively responding, the cats pressed the bar at a relatively constant rate. During the fixed-price schedules, Bill's eating rate increased and Presto's eating rate decreased somewhat as price increased; the eating rates did not vary systematically across variable-price schedules (Figure 2).

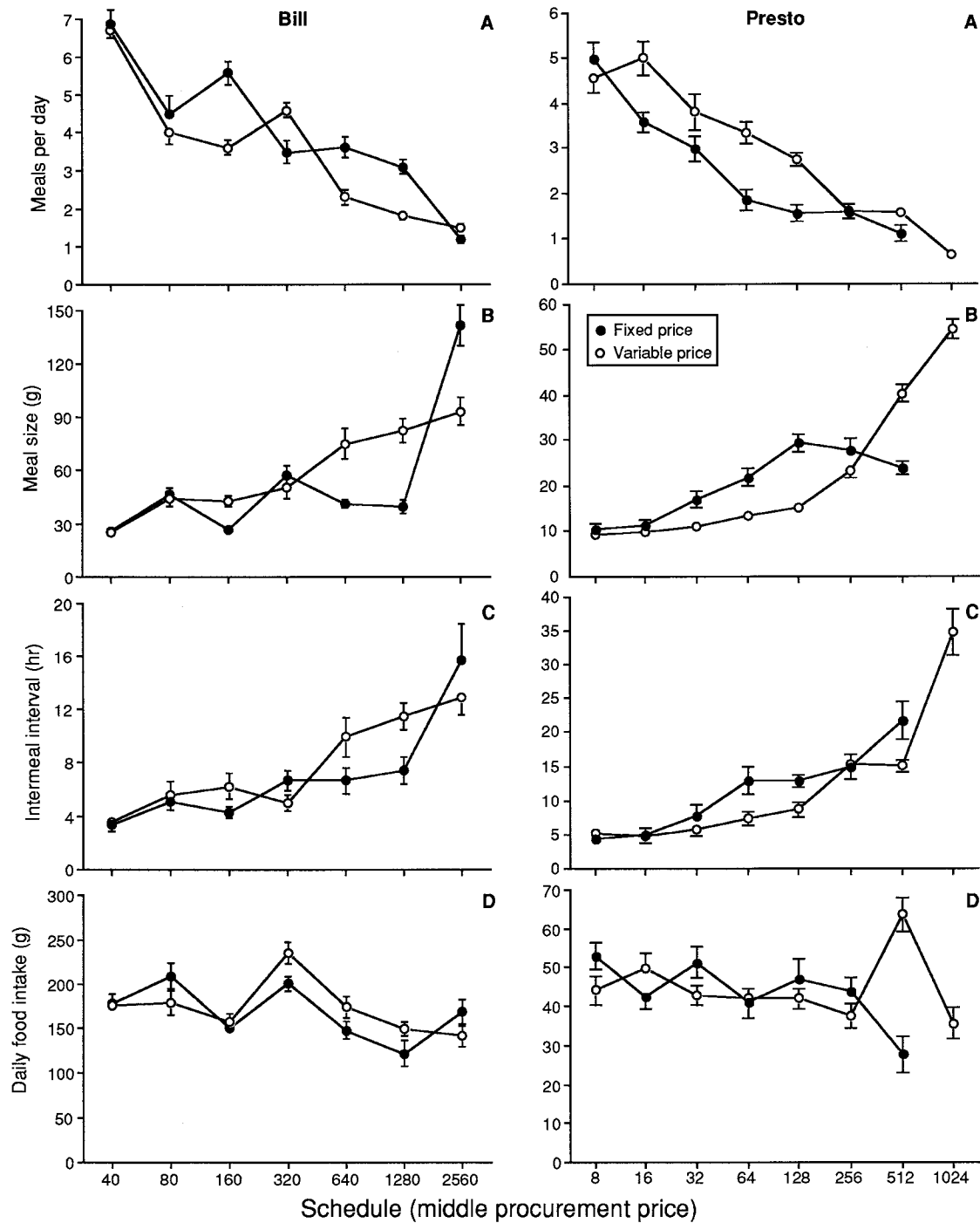


Fig. 1. Mean (\pm SE) meal frequency (A), meal size (B), intermeal interval (C), and daily food intake (D) for Bill (left panels) and Presto (right panels) when encountering fixed or variable procurement prices.

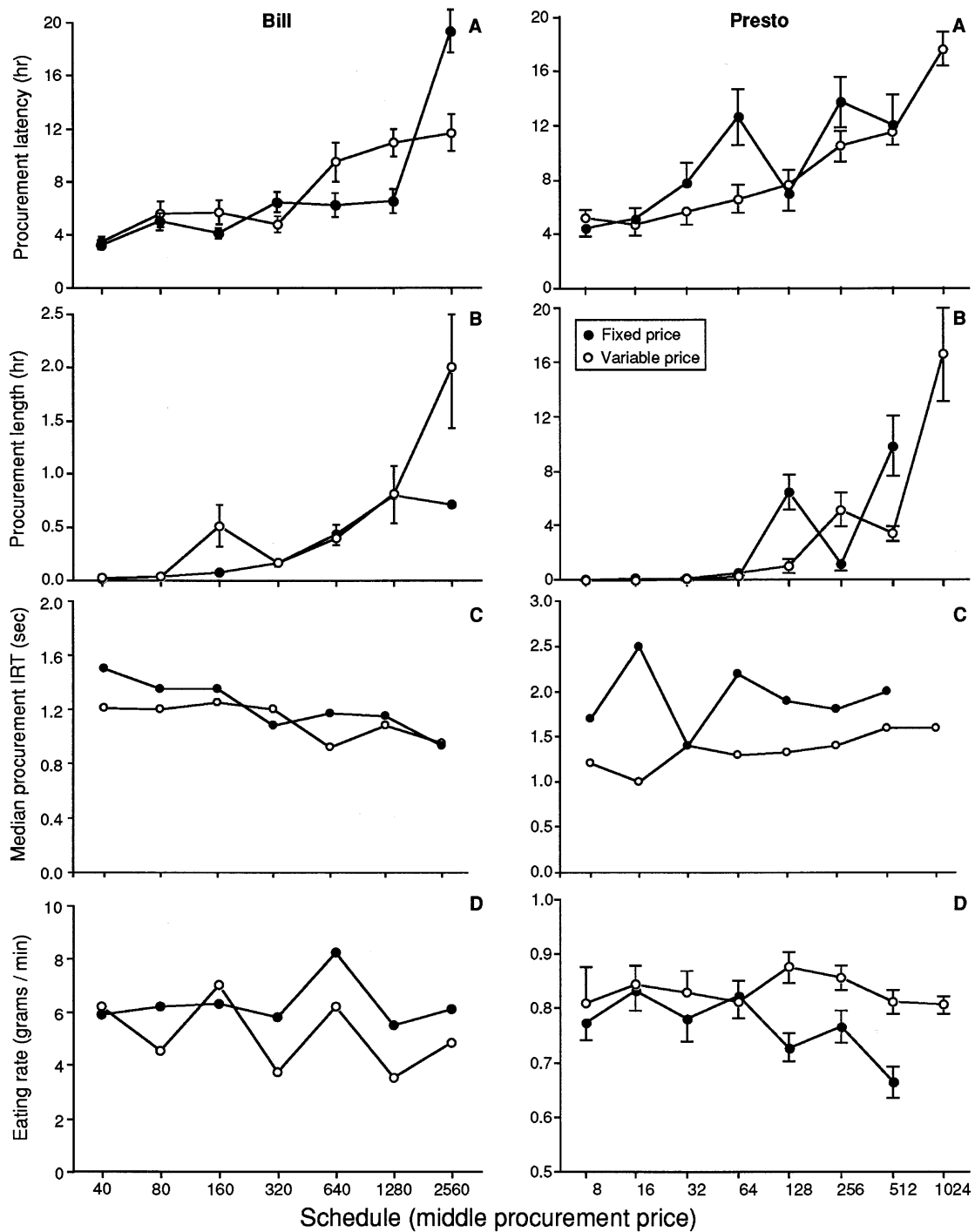


Fig. 2. Mean (\pm SE) latency to begin procurement (A), mean procurement length (B), median interresponse time (IRT) (C), and mean eating rate (D) for Bill (left panels) and Presto (right panels) when encountering fixed or variable procurement prices. Standard error bars are not shown in the case of Bill's eating rate because it was estimated for each schedule by dividing total grams consumed by total eating time.

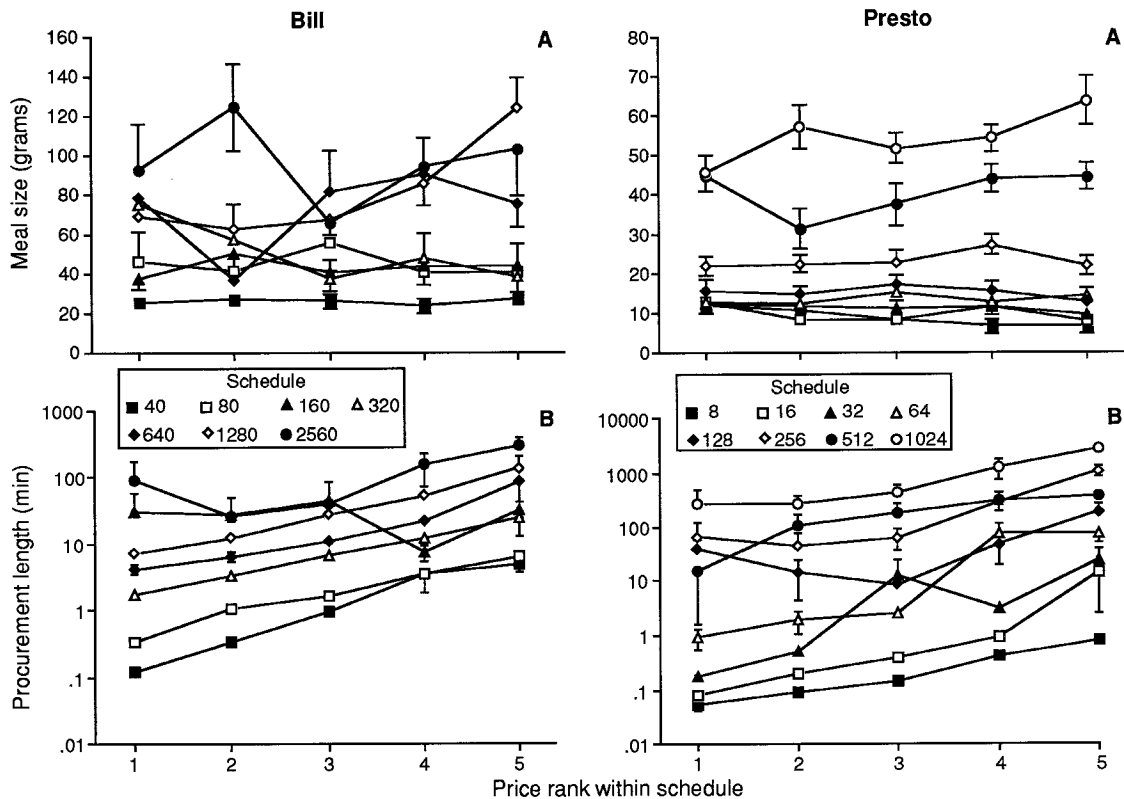


Fig. 3. Mean (\pm SE) meal size (A) and procurement length (B) for Bill (left panels) and Presto (right panels) at each price, ranked from lowest to highest, in the variable-price schedules.

Figure 3 presents the average meal sizes and procurement lengths for each of the five prices, ranked from 1 (lowest) to 5 (highest), in each variable-price schedule. Recall that for Bill, meal size in grams was estimated by multiplying the eating time per meal by the calculated daily eating rate. With the exception of the VR 1,280 schedule for Bill and the VR 1,024 schedule for Presto, meal size was not affected by the price of the meal; higher prices did not predict larger meals. Procurement length was directly related to procurement price for both cats.

Because each price appeared once in each five-meal frame, recent price encounters could have provided some information about the upcoming prices. To determine if the cats' meal sizes were affected by the likely size of the next procurement price, we analyzed the sizes of midpriced meals that occurred after two low-priced meals (when the likely next price would be high) or after two high-priced meals (when the likely next price

would be low). For neither cat were meals sized differently depending on what prices has preceded the middle price (Figure 4).

DISCUSSION

Domesticated cats and rats use the same strategy when foraging in a habitat in which they randomly encounter food patches having different procurement prices: They adjust meal frequency and size to an average of the encountered prices rather than directly to the number of responses made in or the time taken to complete the immediately preceding procurement. This global strategy implies that the cats store information over a relatively long period that encompasses many meals. Because of the inherent variability of meal size, the present data do not make clear whether the animal responds to a moving average that is updated with each encounter, or whether the animal comes to recognize the prices in each schedule and thus responds to

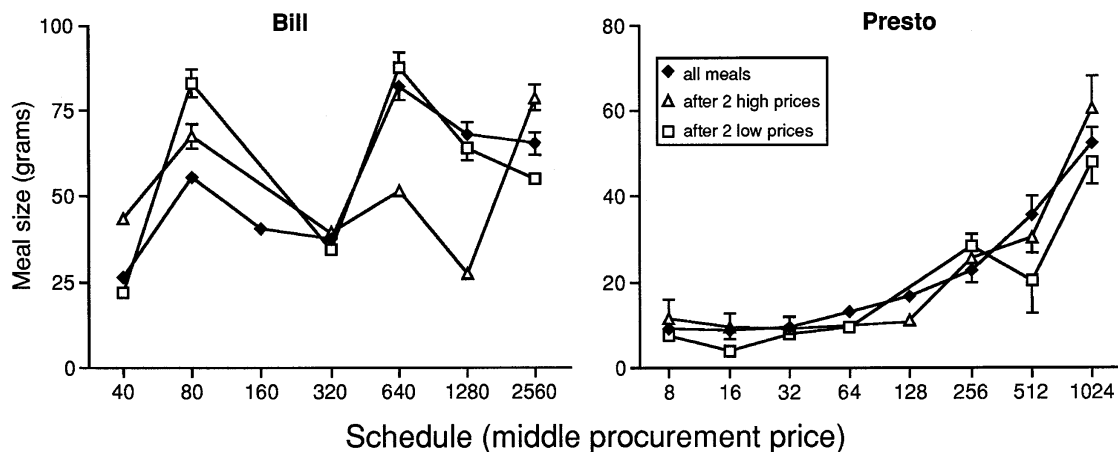


Fig. 4. Mean (\pm SE) meal size of all middle-priced meals in each variable-price schedule and the size of middle-priced meals that were preceded by two low-cost meals or by two high-cost meals for Bill (left panel) and Presto (right panel).

a fixed average for that schedule. Further, we do not know what type of average (e.g., geometric, harmonic) best describes the animal's cost integration. Future studies that impose prices drawn from other than rectangular distributions or use other than geometric series would be instructive.

Conventional wisdom has emphasized the immediate effects of consequences on behavior. For example, the strength of the effect of a reinforcement on a response or on the value of a conditional response in a chain is thought to decay rapidly, or to be devalued (Rachlin, 1992), as a function of delay of reinforcement. The present results suggest that the width of the time window over which consequences can act is substantially longer than previously thought. This view is supported by a recent study (Mathis, Johnson, & Collier, 1995) in which consequences (in this case, access to an large cup of food) maintained a response even when access occurred more than 24 hr after the response. Those results suggest that the notion of consequences embodied in the concept of reinforcement does not apply in simple fashion to closed-economy procedures in which the animal controls the onset and offset of bouts of behavior and does not reflect the capacity of an animal to respond over the long term to the economic structure of its habitat.

In the present case, the magnitude of a response effort and the magnitude of its consequence are not necessarily correlated; the size

of a meal is not determined by the specific time or effort expended to gain access to the food. Instead, meal frequency and size are a *cost-limiting combination* based on average expenditures of time and effort over several meals, even when they occur a day or more apart. This capacity for long-term averaging has not been a central topic in animal learning because it has not often been seen or looked for. The long time window revealed in the foraging paradigm reinforces the argument presented by Timberlake et al. (1988) that we must use multiple measures and convergent techniques to assess the time window over which habitat variables may influence behavior.

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